A communication was read from the Rev. Thomas R. R. Stebbing and Mr. David Robertson containing the descriptions of four new British Amphipodous Crustaceans. These were named *Sophrosyne robertsoni*, *Syrrhoë fimbriata*, *Podoceropsis palmatus*, and *Podocerus cumbrensis*. Of these, *Sophrosyne robertsoni* belonged to a genus first observed at Kerguelen Island.

This paper will be printed entire in the Society's 'Transactions.'

The following papers were read:—

1. On the Subdivision of the Body-cavity in Lizards, Crocodiles, and Birds. By Gerard W. Butler, B.A. (Communicated by Prof. G. B. Howes, F.Z.S., F.L.S.)

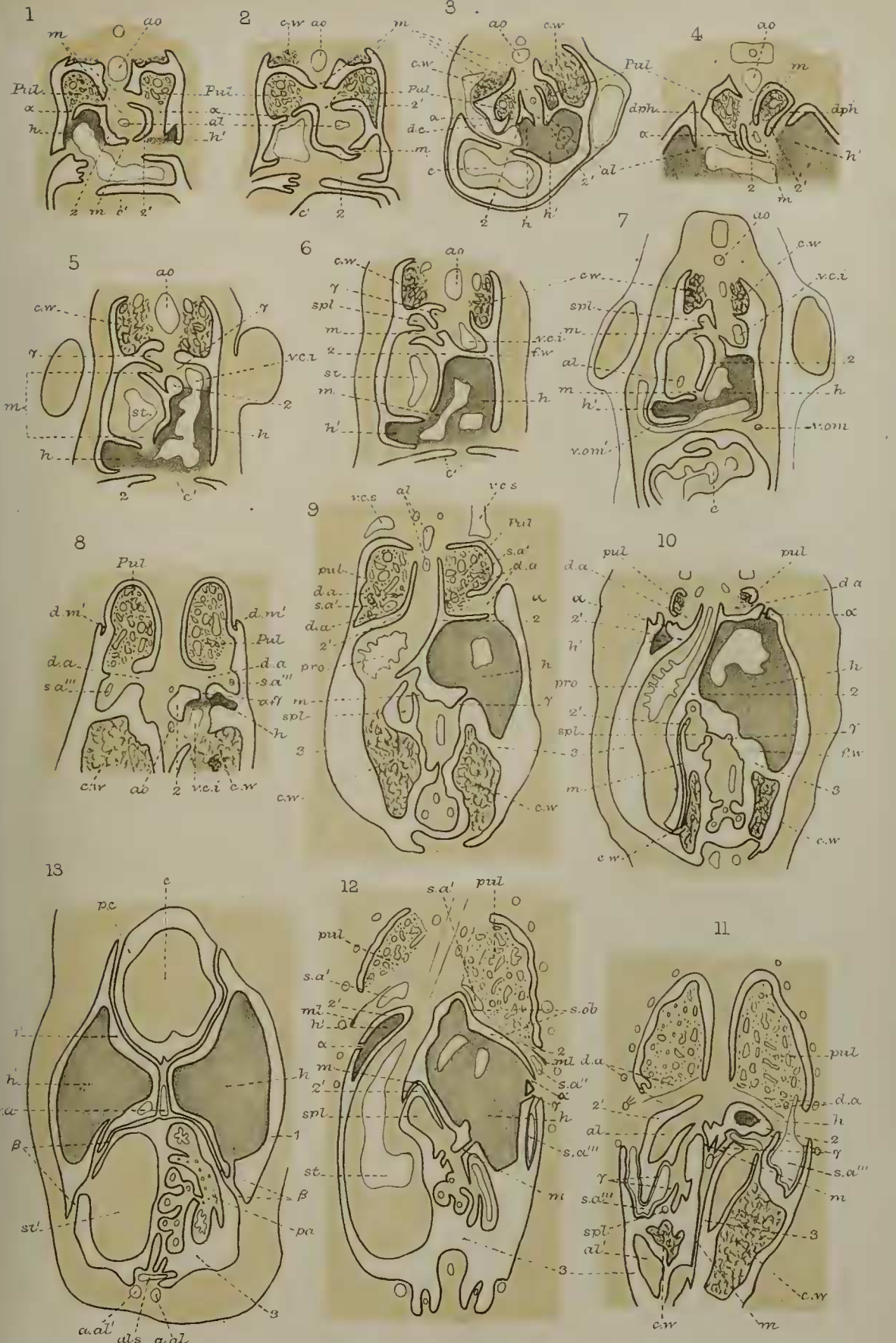
[Received November 14, 1889.]

(Plates XLVI.–XLIX.)

Contents. Page

I. Introductory.

There are embodied in this and another communication on the "Relations of the Fat-bodies of the Sauropsida" (see below, p. 602), the results of some months' work, carried on in the Biological Laboratory of the Normal School of Science and Royal School of Mines, at the instigation of my teacher, Prof. G. B. Howes. To him my best thanks are due for most of the material employed, and still more for the time and trouble which he has always been ready to devote to furnishing me with suggestions and advice. For lesser gifts of specimens I have to acknowledge my indebtedness to Dr. A. Günther, F.R.S., to Mr. G. A. Boulenger, to Prof. Wiedersheim of Freiburg, and to my fellow-student, Mr. E. W. L. Holt. Mr. Boulenger has, moreover, on various occasions kindly furnished me with welcome information.



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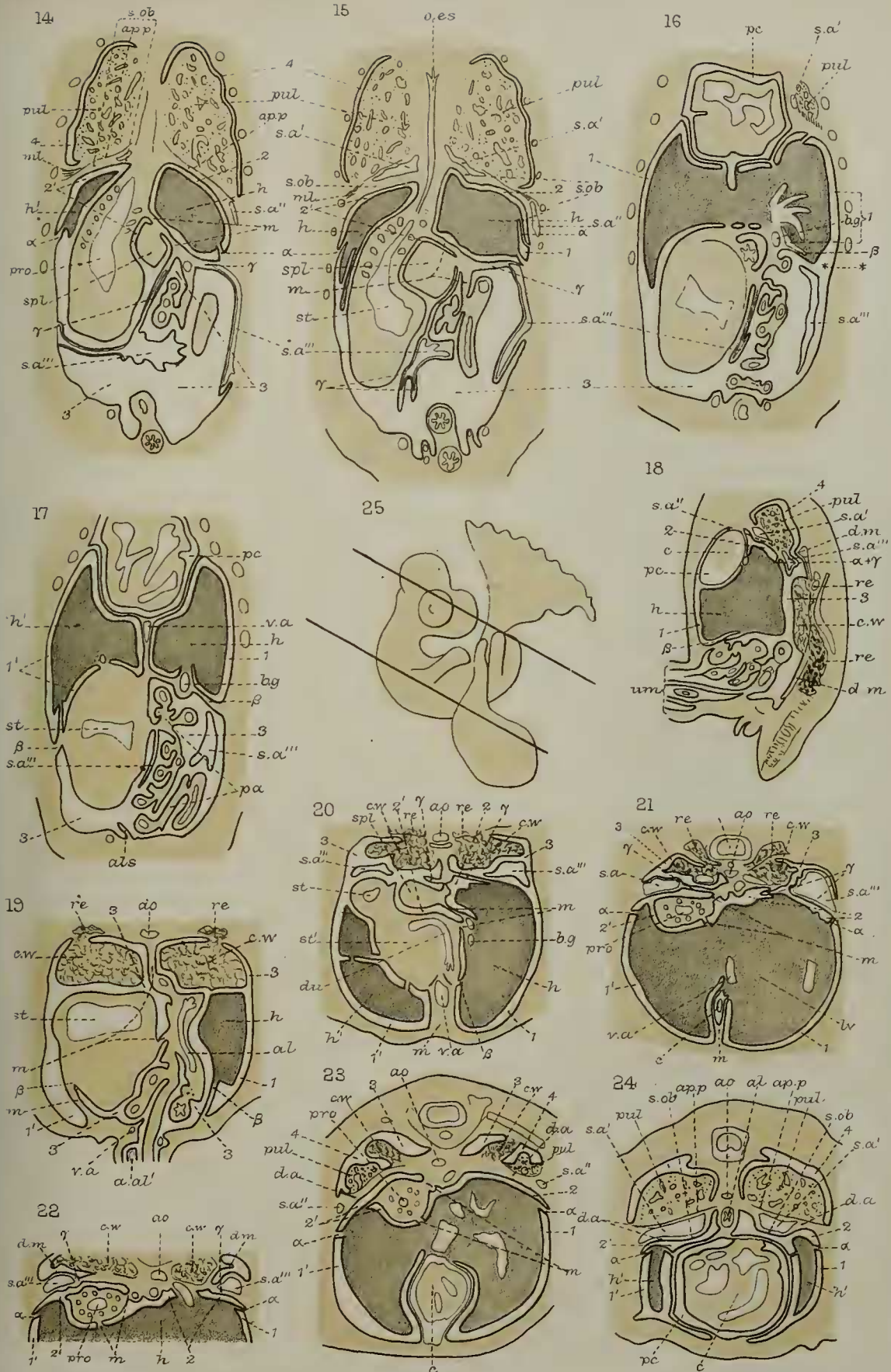

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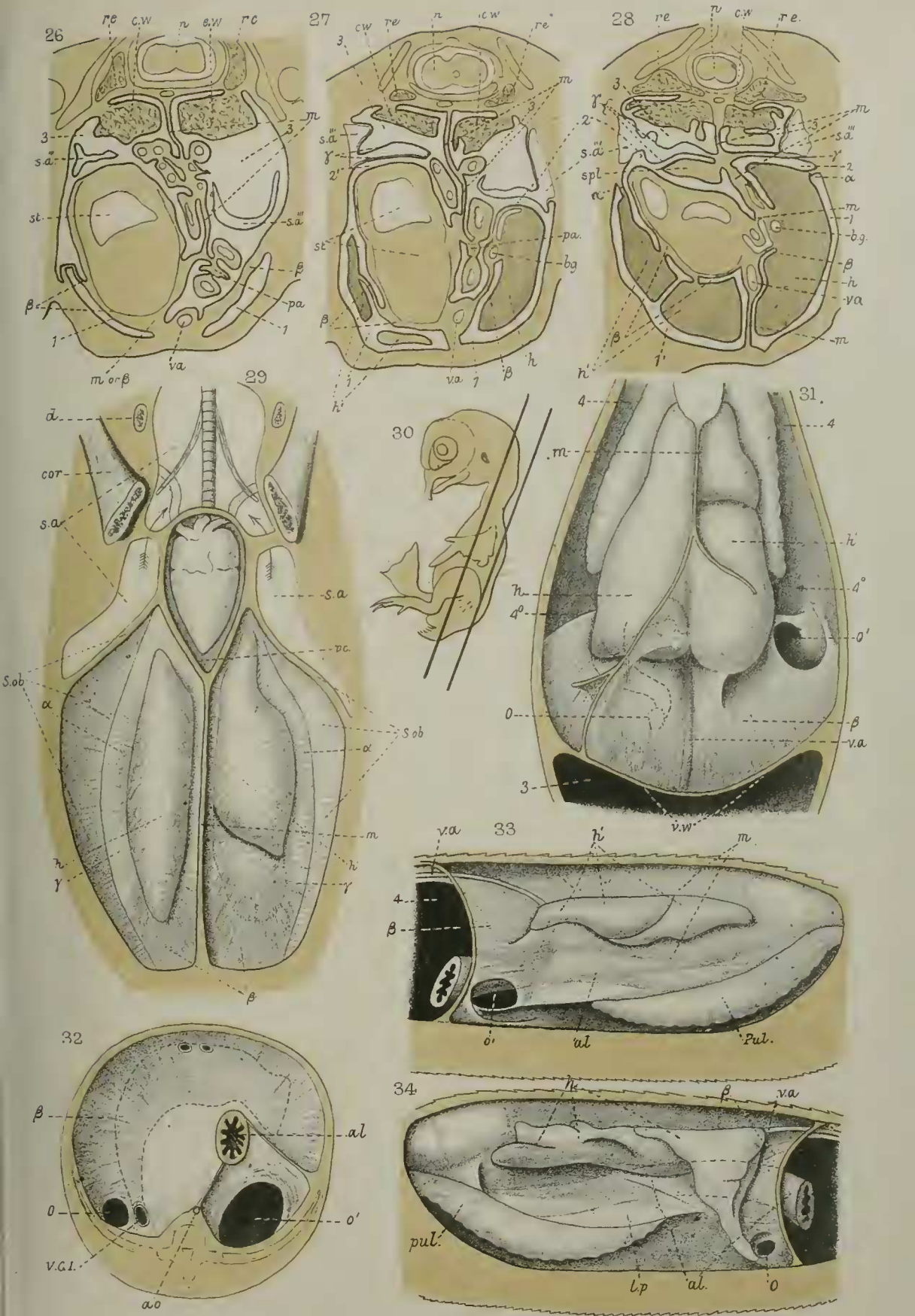

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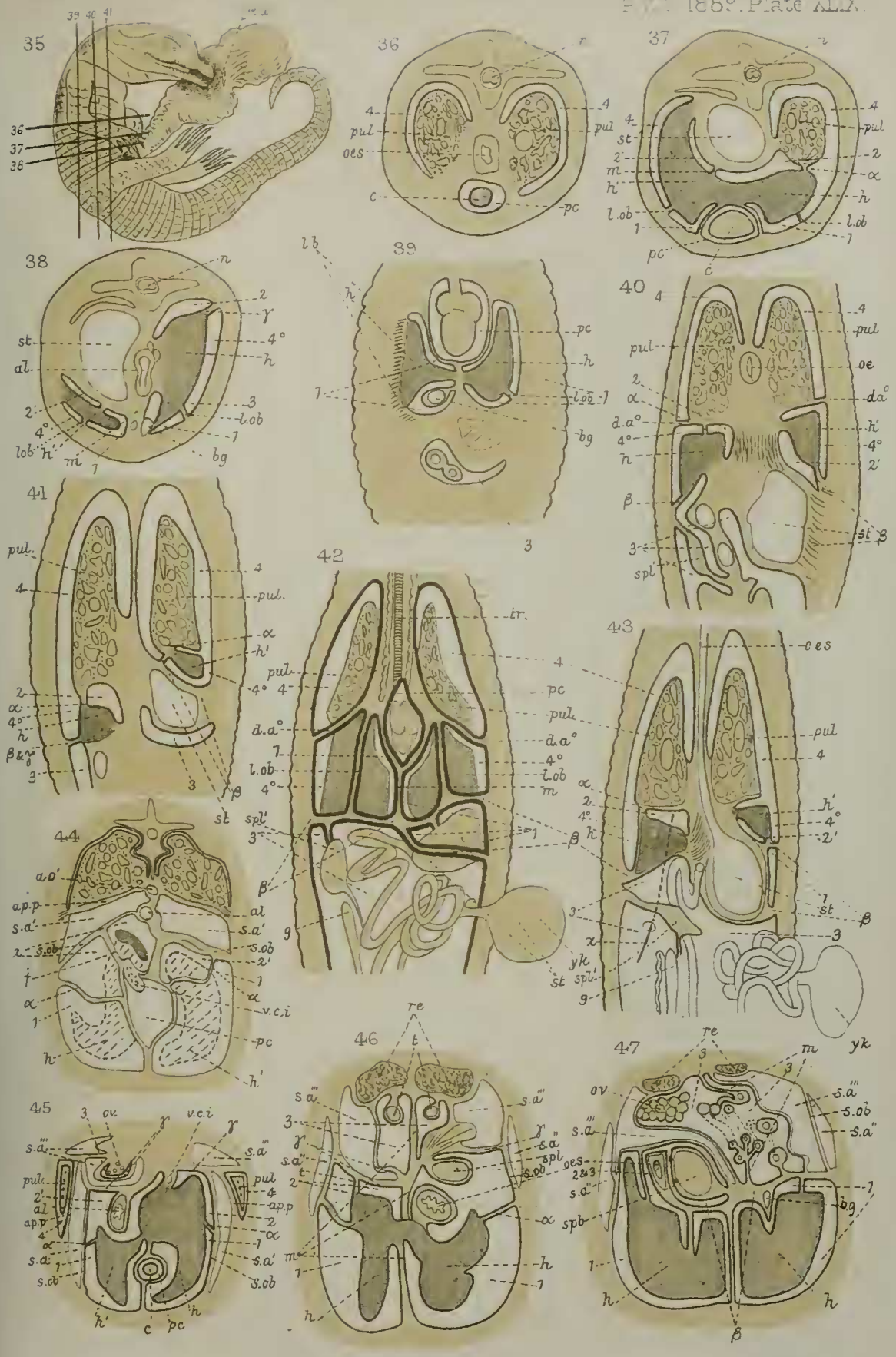

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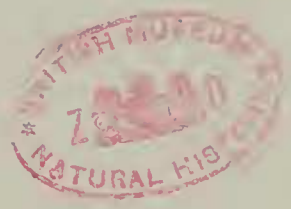
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Nothing appears to be known of the development of the subdivisions of the body-cavity in the Crocodile, and to treat the subject of this paper satisfactorily the writer should have a familiar and personal acquaintance with not only that, but with the whole corresponding course of development, in Mammal, Bird, and Lizard, so far as the partial or complete septa in the body-cavity are concerned.

I have followed the development in the chick down to the twelfth day by means of complete series of consecutive sections taken in different planes, and particularly during the latter half of this period; but I cannot pretend to an equal acquaintance with the development in Mammalia, and in common, as I believe, with other observers, I have not been able, in the case of the Lizards, to compare the development in *Varanidæ* or *Teiidæ* with that in *Lacertidæ*.

Nevertheless it may be well at the present stage to make known in a preliminary paper certain observed facts, and to indicate certain homologies which they suggest.

I append a list of the more noticeable of the papers bearing on this subject to which I have referred; but, while acknowledging indebtedness to the authors of the same, I do not attempt a *résumé* of their contents; but, except in those cases where reference is made to any of them, confine myself to sketching the facts from my own observation, and to stating the conclusions to which they appear to point.

Certain subjects, such as the later stages in the development of the Avian diaphragm, and the formation of the air-sacs, as from the sixth to the twelfth day of incubation in the Fowl, and the relations and homologies of the various ligaments and septa about the liver-lobes in Birds and Reptiles, do not seem previously to have received full attention.

The consideration of these and of certain other points seems to show that the complication of the membranes in the adult Bird and Crocodile can, to a greater extent than might be imagined, be analyzed and expressed in terms of structures found in other Reptiles, where the arrangement is simpler.

II. On the Subdivision of the Body-cavity in the Adult Fowl.

On carefully cutting away the sternum and ventral body-wall of a Duck or Fowl, we see that the liver-lobes for the most part lie in two sacs entirely shut off from the rest of the body-cavity (*cf.* Plates XLVIII. and XLIX. figs. 29 and 44–47, *h*, *h'*; l, l'). These sacs are bounded ventrally by the sternum, externally by the vertical portion of the "oblique septum" of Huxley (*s.ob.*), mesially by the median ventral ligament (*m*) and posteriorly by the "omentum" (β), which passes anteriorly into the hinder portion of a transverse septum (γ) ventral to the abdominal air-sacs[1]. Not much, however,

[1] Huxley appears to me to have included this transverse septum (γ) in his "oblique septum," while Perrault appears to have described the two elements β and γ (just referred to separately, by reason of their arising quite separately in the embryo) as the "*diaphragme transversal*." Sappey (1, p. 35) says, speaking of

of this latter septum enters into the dorsal wall of the sacs in question, for the anterior portion of this wall is formed by the liver-lobes (*h*, *h'*) themselves, and by the ligaments (*a*, *a*) which pass from the liver to the more vertical portions of the "oblique septum." The lines of attachment of these ligaments to the oblique septum follow approximately the ventro-external margins of the lungs, where this latter membrane is apposed to them. The ligaments referred to may be called the *pulmohepatic ligaments* (*a*, *a*). I now call special attention to them because in the sequel I use them as a landmark in comparing the different types.

On cutting through the pulmohepatic ligament there is exposed, on the right side, another entirely closed sac (Plate XLIX. figs. 44, 45, 46, 2), bounded externally by the more vertical portion of the "oblique septum," dorsally by the septum (γ) above referred to, and in part by the more horizontal portion of the "oblique septum." The right liver-lobe (*h*, figs. 44 & 46) is attached to the dorsal wall of this sac from the point where the vena cava inferior enters it, backwards, and the sac is thus partially subdivided into two.

In the Duck, the corresponding sac of the left side appears to be quite closed; but it really communicates with the post-hepatic or intestinal portion of the body-cavity by a small aperture, which is merely closed by the left "abdominal" air-sac flapping against it.

In the Fowl, however, the continuity of this sac with the intestinal cavity is plain, its hinder end being freely open.

These two sacs in the Bird, which are partly bounded by the pulmohepatic ligaments ventro-laterally, I will call the *pulmohepatic recesses*, and their homologies will be referred to later (p. 460, § III. *c*). For a capital description of the avian diaphragm reference may be made to Sappey (1, pp. 21–26), also to the 'Comparative Physiology' of Milne-Edwards (vol. ii. p. 401) and to Huxley (4). All three accounts accord perfectly. Milne-Edwards's, in fact, differs little from Sappey's, even in nomenclature. Huxley introduces a few new terms, such as *pulmonary aponeurosis* (for the *plan transversal* or *diaphragme pulmonaire* of Sappey, the *diaphragmite antérieure* of Milne-Edwards), and *oblique septum* (for the *plan oblique* or *diaphragme thoraco-abdominal* of Sappey, *diaphragmite postérieure* of Milne-Edwards). I here use Huxley's terms for these two parts of the diaphragm. I assume that the general relations of these two membranes and their air-sacs, which he and Sappey have so clearly described, require no explanation on my part. Sappey makes it very clear that he regards the two membranes

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the abdominal air-sacs, "En bas et en avant ils s'appuient sur une cloison fibreuse qui divise chez tous les oiseaux la cavité abdominale en deux cavités plus petites, l'une antérieure, qui représente l'abdomen et qui loge le foie, l'autre postérieure, qui représente le bassin et qui loge l'estomac et les intestines; cette cloison fibreuse extrêmement remarquable dans l'autriche où elle a été décrite par Perrault sous le nom de diaphragme transversal, s'insère à toute la circonfereuce des os du bassin, et soutient l'estomac ainsi que le tube intestinal."

It will be noted that the two sacs I am describing form only the ventral portion of the anterior cavity of which Sappey here speaks.

referred to, between which lie the two pairs of air-sacs that he calls *réservoirs diaphragmatiques* or *moyens* (*intermediate air-sacs* of Huxley), as constituting a single diaphragm; and Milne-Edwards says (*loc. cit.*), "l'appareil diaphragmatique des oiseaux se compose de deux portions ou diaphragmites." This unity of the whole apparatus, which is very apparent when the development is followed (*cf.* § III.), cannot, I think, be too clearly kept in view, especially when homologies are being discussed.

In this paper I refer to all from the anterior or dorsal face of the pulmonary aponeurosis to the peritoneum covering the posterior or ventral face of the oblique septum, as the *Avian diaphragm*, in contradistinction to the Mammalian diaphragm, with which, in agreement with Huxley's verdict, it is argued in the sequel it has little, if any, true homology.

With regard to the term "oblique septum" of Huxley. As he speaks (p. 562) of the four post-bronchial air-sacs of either side as being shut off by the "oblique septum" in a similar kind of way, I presume that he includes under this term the septum (γ in the Plates) dorsal to the liver, above referred to. At all events in using this term, I refer merely to that septum which in the Fowl is (*cf.* p. 458), so to speak, blown away from the other part of the Avian diaphragm by the growth of the intermediate, or diaphragmatic, air-sacs.

I would call this septum (γ), which on either side forms the dorsal wall of the pulmohepatic recess, and into which a large part of the abdominal air-sac projects[1], the *oblique abdominal septum*. It is true that the more lateral parts of this septum, in that they take their final form in connexion with the abdominal air-sac, might so far be held to resemble the "oblique septum" proper, in its relation to the diaphragmatic air-sac; but this would not apply to the more median parts of the septum (γ), and the nature of the two things is really very different. That which I have termed the *oblique abdominal septum* does really separate one part of the body-cavity from another, as described bySappey(footnote, p. 454 above), and is covered on both sides by peritoneum; but the "oblique septum" is only part of a cœlomic septum, the other part being the pulmonary aponeurosis.

The *oblique abdominal septum* we might perhaps regard as a backward continuation of the *whole avian diaphragm* with the abdominal air-sacs between its dorsal and ventral laminæ, just as the intermediate or diaphragmatic air-sacs lie between the two laminæ of the latter.

III. On the Development and Homologies of the various Septa in the Body-cavity of the Chick.

We may now turn to consider the development of the septa in the body-cavity of the Fowl, to which reference has been made in the preceding section.

[1] Sappey (see footnote, p. 454) says that these air-sacs *rest on* (s'appuient sur) the septum in question; but it is more correct to say that they *project into* it, in the end, as it were, blowing away a dorsal lamina from the rest.

No attempt will be made to go over the work that has been done on the earlier stages of the chick down to the 6th day of incubation, but rather to consider the light thrown on the adult condition by the subsequent stages of development [1].

The changes going on, *for the most part synchranously*, in the chick between the sixth and twelfth days may be grouped, so far as the subdivision of the body-cavity is concerned, under the following heads [2]:—

(A) The completion of the *avian diaphragm* and the development of the "diaphragmatic" and "abdominal" air-sacs (*s.a'*, *s.a''*, and *s.a'''*).

(B) The development of the *oblique abdominal septum* (γ), partly in connexion with the growth of the "abdominal air-sacs."

(C) The lateral extension of the ventral ligament of the stomach and hinder part of the liver (avian "*amentum*," β), so that meeting the *pulmohepatic ligaments* (α) and the *oblique abdominal septum* (γ), it on the one hand helps in the closing of the ventral liver-sacs (1, 1), and on the other in the formation of a *post-hepatic septum* ($\beta+\gamma$) ("diaphragme transversal" of Perrault), which is, however, not complete on the left side.

(D) The assumption of their final form and relations by the *pulmohepatic recesses* (2, 2') and *ligaments* (a, a).

III. (a). *On the Development of the Air-sacs in relation to the parts of the Avian Diaphragm.*

On the 8th day, while the passages between the pleural and peritoneal cavities are widely open, the abdominal air-sac first

[1] The following remarks, however, may be added with regard to the shutting-off of the pericardium. The works referred to at the end of this paper, and others, seem to show that the shutting-off of the anterior portion of the pericardial and pleural cavities from each other arises in a similar way in Mammals and Birds, in connexion with the ducts of Cuvier; while, on the other hand, such similarity cannot be claimed for the two classes in the matter of the closing-off of the posterior part of the pericardium from the rest of the body-cavity. In birds the closing-in of the pericardium posteriorly and postero-dorsally takes place, it appears, comparatively late; and finally in the adult we have the pericardium bulging into the peritoneal cavity, with little besides the peritoneum covering its postero-dorsal surface. In connexion with this subject, reference may be made to the recent paper by Strahl and Carius (9), where it is stated that in Mammals the part of the body-cavity which, later, forms the pericardial and pleural cavities arises distinct from the rest in the region of the "proamnion," and that it becomes secondarily connected with the posterior part of the cœlome (a subsequent separation of course taking place). These observers assert, as a further noteworthy distinction between that portion of the cœlome which in Mammals forms the pleural and pericardial cavities, and the corresponding part in Birds, the fact that in the former it is closed laterally, or on what is, when folding round of the sides takes place, the ventral side, whereas in the latter it is not so closed, but passes off into the extraembryonic cœlome. Thus from the first the thoracic cavity would seem to be much better marked off in the case of Mammals than in that of Birds.

[2] The references in brackets are to the parts so indicated in the various figures on the Plates.

becomes observable as a bronchial cavity at the outer postero-dorsal corner of the lung. It lies in the mesoblastic tissue, which later develops into the avian diaphragm ("pulmonary aponeurosis" + "oblique septum"), but which at this date cannot be distinctly marked off from the mesoblast of the lung itself.

During the first half of the 9th day (see Plate VIII. fig. 8) the abdominal air-sacs (*s.a'''*) have the appearance of oval cavities within somewhat conical outgrowths of the diaphragmatic mesoblast (*d.a*).

At the beginning of the 10th day, when the separation of the pleural and peritoneal cavities is about completed[1], the abdominal air-sacs project to a considerable extent posteriorly into the peritoneal cavity (*cf.* figs. 11, 12, and 20, *s.a'''*), while more anteriorly (*cf.* left side of fig. 11 and figs. 21 and 22) they lie within the *oblique abdominal septum* (γ, γ), which assumes its final form only in connexion with them.

At the beginning of the 12th day (*cf.* figs. 14, 15, 27, and 28) we find that the abdominal air-sacs not only have increased in size and extended more into the septum referred to, separating its two layers of peritoneum, but that they have begun to, as it were, strip off the peritoneal covering of the body-wall by extending behind it; and this process goes on till in the adult (*cf.* fig. 47) comparatively little of the peritoneal lining of the intestinal portion of the cœlome remains applied to the body-wall.

The first beginnings of the "anterior-" and "posterior-intermediate" air-sacs are not quite so easy to trace. The former is conspicuous in the latter half of the 8th day, and both can be made out on the 9th. (The anterior intermediate sacs are shown in fig. 9, *s.a'*.)

At the beginning of the 10th day when, as stated above, the *avian diaphragm* forms a complete partition, one can, in stained sections, distinguish two layers (which do not, however, exactly correspond to the two diaphragmatic septa of the adult) (*cf.* figs. 11, 12, and 24). In the region of the ribs the muscles (*ml*) of the future pulmonary aponeurosis, or "costopulmonary muscles" of Huxley, are indicated, and from this region a darkly staining layer extends inwards to the middle line passing dorsal to the œsophagus (*cf.* fig. 24, *ap.p*). This darkly staining layer together with the above mentioned developing muscles indicates the "pulmonary aponeu-

[1] It must be remembered that the dates in the case of the development of the chick are not absolute indices. As is well known, the rate of development under artificial incubation may differ considerably from that under a hen, and also in the case of different eggs artificially incubated. I have seen the peritoneal not closed off completely from the pleural cavities in a chick said to have been artificially incubated for 11 days; and this agrees with Uskow's observations (5, p. 205). He remarks that a connexion between the pleural and peritoneal cavities exists on the 12th day. Yet, in the specimen naturally incubated, 9 days 1 hour (beginning of the 10th day), of which longitudinal horizontal sections are shown in figs. 11–13, no such connexion was to be made out in a continuous series of sections. So far as the stages illustrating the development of the air-sacs go (8th–12th days), I have taken as my standard a series of naturally incubated embryos.

rosis," while the "intermediate" or "diaphragmatic" air-sacs lie posterior to this in a layer of tissue which, at this stage, forms the thicker element of the *avian diaphragm*.

At the beginning of the 12th day (*cf.* Plates XLVI., XLVII. figs. 14 and 15) we find that these air-sacs have increased in proportional size. Compare, for instance, the relative extent of the anterior diaphragmatic sacs (*s.a'*) in figs. 12 and 15, which are taken through an approximately corresponding region of embryos of the 10th and 12th day respectively.

As these air-sacs develop, they, so to speak, split the layer of the diaphragm in which they lie, part going, with the darkly staining layer and tissue in front, to form the "pulmonary aponeurosis," and part, that lies postero-ventrally to the air-sacs, forming the "oblique septum." In the end the two air-sacs referred to come into contact, and any membranous diaphragmatic tissue that may lie between the apposed walls is quite insignificant.

The avian diaphragm is thus seen to be completed as a single structure, and its separation into its two laminæ is a secondary detail arising in connexion with the development of the two pairs of intermediate or diaphragmatic air-sacs, which first penetrate it at a time when no distinct line can be drawn between the tissue that goes to form it and that of the developing lung itself.

III. (*b*). *Certain previous Opinions with regard to the Avian Diaphragm.*

With regard to the question of the homology, if any, between the Mammalian and Avian diaphragms, Sappey, whose most excellent monograph on the respiratory apparatus of the adult bird (1) was published in 1847, expresses his opinion as follows (p. 21) :—"Dans les oiseaux le diaphragme comprend deux plans qui se confondent à leur point de départ, mais s'isolent bientôt pour suivre l'un une direction transversal, l'autre une direction oblique." ..... "Le premier a pour analogue dans l'homme et les mammifères toute la partie de ce muscle qui s'insère à la face interne des côtes ; le second représente les piliers du diaphragme ;" and he gives his reasons for regarding the attachment of the paired partly muscular fibrous tracts in the anterior dorsal region of the oblique septum as homologous with those of the pillars of the diaphragm to the lumbar vertebræ. The presence or absence and the distribution of muscle-fibre seems to have considerable weight with him and others in dealing with questions of homology[1]; and with this the questions of nerve-distribution must be also considered.

With regard to this latter, Sappey says (1, pp. 25 and 26) that (what Huxley afterwards called) the "pulmonary aponeurosis" is supplied from the intercostal nerves, and suggests that this mode of supply is similar to that by the phrenic nerve, both being by branches

[1] The question is apt to present itself, however, is muscle-fibre of great importance in such a case? Might we not have a septum homologous to the mammalian diaphragm without any muscle developed in it at all, simply consisting, so to speak, of the pleural and peritoneal membranes back to back?

from spinal nerves; while the nerves that supply the muscle in the antero-dorsal region of the "oblique septum" seem comparable to parts of the sympathetic of Mammals, in which group the diaphragm is partly supplied from the solar plexus[1].

Uskow (5, p. 214), in giving a *résumé* of the different types of diaphragm, says that the condition in Man is like that in the Rabbit, except that a part of the diaphragm is fused with the pericardium; and that the diaphragm of the Fowl is the same as that in Man, but the diaphragm has no muscle, and its ventral portion is entirely fused with the substance of the pericardium.

I do not, however, think, in the light of the clear description he gives elsewhere of the important differences between the mammal and bird, in the regions of the diaphragm (see below p. 462), that such remarks are necessarily to be taken as implying a belief in an approximate morphological homology.

Huxley, on the other hand (4, p. 567), says "neither in Apteryx nor in any other bird has either of these [pulmonary aponeurosis and oblique septum] the slightest real resemblance to a Mammalian diaphragm. For, as has been seen, the heart lies altogether behind both, and the muscular digitations of the pulmonary aponeurosis are supplied by the intercostal nerves, the phrenic being absent. The vertical and oblique septa[2] really answer to the fibrous tissue of the posterior and middle mediastinum in Mammals. In this, as in all other cases, the meaning of ornithic peculiarities of structure is to be sought, not in Mammals but in Reptiles." And he goes on to mention certain avian characteristics which are elsewhere only represented in Reptiles, and to compare the Crocodile with the Bird.

Huxley's verdict on the question of the diaphragm, as thus tersely stated, failed to remove the suspicion that while the more central part of the avian diaphragm doubtless corresponded to mediastinal tissue, a considerable portion thereof, more lateral in position, might be homologous with the diaphragm of Mammals. And it was only after reading Ravn's paper (9), in which, pp. 139–147, he goes at some length into the development of what His

[1] A rather similar line of reasoning occurred to the writer independently. For instance, in investigating the nature of the nerve-supply, the question at once presented itself—Where is one to look for the homologue of the phrenic nerve? What is the phrenic nerve? In Mammals it appears as a specialized trunk (supplying a specialized muscle), composed of factors from a rather indefinite number of spinal nerves of the cervical region. But seeing that there is this indefiniteness, and that the division into regions (thoracic, cervical, &c., &c.) of the vertebral column in Birds and Mammals is so very different, a definite answer was not reached. I was rather inclined, however, to regard as possibly to be reckoned in the same series with the phrenic nerve, those nerves which are connected with the spinal nerves in the thoracic region (of the Duck) rather after the manner of the sympathetic, and which, I presume, are the nerves referred to by Sappey, in his second category, as supplying fibres to the "oblique septum." In spirit-specimens, however, I did not detect any nerve-fibres passing from them to that structure.

[2] It will be noticed that he does not refer to the pulmonary aponeurosis with the oblique septum as homologous with the mediastinal tissues.

named the "recessus superior sacci omenti" in Mammalia, whose homologues in the Bird are much more conspicuous, that it occurred to me that these recesses and their bounding walls might serve as landmarks, and enable us more definitely to contrast the diaphragmatic structures in the two classes (*cf. infra*).

III. (*c*). *On the Development of the Pulmohepatic Ligaments and Recesses.*

In this connexion it will be convenient to consider the developmental changes in the chick classed under head (D) on p. 456.

Referring to figures 1–4 (of which 1 and 2 are transverse sections of a 6th-day chick, 3 of an embryo of *Lacerta vivipara*, 4 of an embryo mammal[1]), we see running down the centre of the sections the median vertical sheet of tissue (*m*) which in all the types under consideration forms a complete vertical septum in the thoracic and anterior abdominal regions. On either side of it are set the lungs and the two halves of the liver, while the alimentary canal runs in its midst.

It will further be noted that in all three cases the right liver-lobe is attached to the lung of its own side by a vertical ligament (α), which closes on the outside a space (2). The latter is blind anteriorly and opens into the general peritoneal cavity behind.

In fig. 1, which is a section anterior to fig. 2, we see that in the chick there is, on the left side also, a corresponding ligament (α) and included recess (2′), while in the case of the Mammal and (in this instance) of the Lizard there is no such ligament traceable on the left side, and therefore no recess, properly speaking, though 2′ in figs. 3 and 4 marks where it should be. Now the recess on the right side (2) is the "recessus superior sacci omenti" of His, as quoted by Ravn (9, p. 141), and the ligaments (α) are those which in the Bird can be clearly traced developing into the *pulmohepatic ligaments*; while the recesses, with the addition on the right side of all that remains of the omental sac proper, develop into the *pulmohepatic recesses*.

According to Ravn (*op. cit.* figs. 15, 16, and text) this "recess" on the right side is continuous with the main omental sac as late as about the 15th day in the Rabbit, but by the 17th day (p. 146) it has become constricted off from the latter cavity and persists as a separate closed peritoneal sac, which comes to wrap round the œsophagus.

By a reference to the Plates, the development, in the chick, of these *pulmohepatic recesses* and *ligaments* may be followed. Figs. 1 and 2 are transverse sections of the 6th day (and the relations are much the same even on the 4th day). Figs. 5, 6, 7 may be called transverso-longitudinal sections (*cf.* fig. 25) of a 7th day embryo. Of these fig. 6 shows the foramen of Winslow (*f. W.*) leading from the main peritoneal cavity into the sac (2) of the right side, part of which corresponds to the omental sac of Mammals.

[1] See also figs. 6–9, 11, 12, 14–18 of Ravn's paper (9).

Figs. 8, 9, and 10 show this right-hand sac at the beginning of the 9th day, and we see (fig. 10, *f. W.*) that the foramen of Winslow is still open. But on the 9th day this foramen becomes closed (that is, I could find no aperture in a complete series of sections of a chick of 9 days 1 hour incubation), and moreover that part of the recess which surrounds the gizzard, as opposed to the œsophagus, becomes obliterated[1] (compare fig. 12, 2, with fig. 10, 2),

This space (2), which can be followed through the sections of the 12th day (*cf.* figs. 14–17 and 26–28) and seen in those of the adult fowl (figs. 44–46), corresponds, as stated, to rather more than the "recessus superior sacci omenti" of Mammals, since its posterior part represents a portion of the omental sac. For this reason, and because there is a similar space on the left side (where there is no omental sac to have a recess), and because these spaces are in fact no mere diverticula of the omental sac, but have a distinct origin, I have spoken of them as the *pulmohepatic recesses* (*cf. ante*, p. 454). This name expresses their relation to the liver and respiratory organs, and to the pulmohepatic ligaments which form part of their outer wall.

In the fowl the foramen of Winslow up to the 9th day, when it closes, has precisely the same relations as in Mammals, being bounded by the inferior vena cava antero-dorsally, and the duodeno-hepatic omentum, or ventral mesentery that bears the bile-ducts and portal vein, postero-ventrally.

With regard to the corresponding recess on the left side (2′ in the figures previously referred to), a reference to the figures shows that it is from the first in much freer communication with the rest of the peritoneal cavity than that on the right, and the alimentary canal, instead of (as in the case of the other recess) bending round to form, together with the median vertical membrane that supports it (*m*, figs. 9, 12, 14, 15), a posterior or omental wall, appears rather on the contrary to hinder the development of its outer wall by leaning over on the left side between the lung and liver.

III. (*d*). *On the Homology of the Avian and Mammalian Diaphragms.*

On considering the relations of the recesses and ligaments (2, 2′, *a*, *a*) in the two above-named groups, we see that the whole of the Mammalian diaphragm lies laterally or centrifugally to the attachments (*a*, *a*) of the liver to the mediastinal tissues in front of it, while the *avian diaphragm* lies practically entirely within or centripetally to these attachments. So that the condition in birds is expressed by saying that the middle mediastinal tissue of the two sides, instead of coming to wrap round the pericardium, diverges posteriorly and ventrally to become attached to the lateral body-walls[2].

[1] Apparently by constriction off from the rest and the adhesion of its walls.

[2] We may, for illustration, compare the middle mediastinal tissue of birds in its relation to the pericardium to a coat which, instead of being buttoned across the chest (the pericardium), is extended like a wing on either side by laying hold of the front bottom corners.

According to this view, the "avian diaphragm" corresponds, as Huxley says of the oblique septum, to the middle mediastinum of Mammals. The pulmohepatic recesses form a pair of spacious sacs (instead of a single minute one), and the liver is attached to the mediastinal tissue by the pulmohepatic ligaments quite laterally (instead of merely round the œsophagus) along a line on either side very close to that of the attachment of the avian diaphragm itself to the body-wall.

When following the completion of the partition between the pleural and peritoneal cavities of the bird, one observes a ridge which is connected with the Müllerian duct extending inwards from the body-wall to meet the outwardly extending mediastinal tissue. This is at once suggestive of the membrane bearing the Müllerian duct, or its continuation, which in the Amphibia and Lacertilia extends obliquely forwards along the lateral body-wall and ends near the ventral line of division between the lungs and liver. But although the *avian diaphragm* does become attached to the body-wall along the line of attachment of the embryonic Müllerian duct, the fold in connexion with the latter takes, if any, but a comparatively insignificant part in the closing-off of the pleural from the peritoneal cavity.

Uskow (5, p. 204[1]) expressing himself in terms of "Massa transversa"[2] and "Massa longitudinalis"[3], calls attention to just the points of contrast between Birds and Mammals that have been referred to above, viz. the lateral attachment of the liver, the outward diverging postero-ventrally of the mediastinal tissue, with the consequent dorsal as well as lateral projection of the lungs. He notes that the liver projects freely into forwardly extending portions of the peritoneal cavity (pulmohepatic recesses); and he finally states the fundamental difference between the central portion of the diaphragm of the chick of 7 days and the rabbit of 14 days to lie in the fact that in the former it goes with the lungs and in the latter with the liver. But, as remarked above, he goes on rather to compare than contrast the two types of diaphragm, saying (p. 205, when describing a comparatively late stage) so far the rabbit and

[1] "Nicht so bei Huhn. Hier hängt die Massa longitudinalis mit der transversa nicht im medianen Bezirke, sondern nur rechts und links zusammen mit je einem Schenkel. . . . . Sie gleicht also einer medianen Leiste, welche caudalwärts sich in 2 schenkel spaltet; diese fassen einen Kopfwärts vorgeschobenen zipfel der Peritoneal höhle zwischen sich. In diesem zipfel liegt die dorsal fläche der Leber frei. . . . . Nimmt man noch hinzu, das die Lungen in der so beschrankten paarigen Höhle der Pleura nicht nur an den Sagittal rand der massa longitudinalis, sondern vornehmlich auch an die Dorsalfläche der beiden seitlichen Schenkel der Letzteren befestigt sind, so ergibt sich das es nicht leicht ist in den eben erwähnten Bildungen das Mittelstück des dorsalen diaphragmas des Kaninchens wieder zu finden. . . . . .

"Der ganze unterschied zwischen der Entwickelung des Huhns und des Kaninchens kann demgemäss für diese Periode so formulirt werden: Beim Kaninchen legt sich das mittelstück des dorsalen Diaphragmas längs den Dorsalfläche der Leber, beim Huhn längs der Ventralfläche der Lungen an."

[2] Defined *l. c.* p. 171.

[3] Defined *l. c.* p. 172.

the chick are fairly similar, and (p. 214) giving the *résumé* from which a quotation has already been made (p. 459).

III. (*e*). *On the Development of the two Parts of the Post-hepatic Septum of the Bird.*

We have now to refer to the developmental changes grouped under heads B & C (p. 456).

First, with regard to the development of the "*oblique abdominal septum.*"

Ravn (*op. cit.* p. 140) calls by the name of "vena-cava-falte" or "plica venæ cavæ" the ridge that occurs in Mammals as a backward continuation of the embryonic lung-substance, because through it the vena cava inferior passes on its way from the kidneys to the liver and heart. But it will be seen on reference to the Plates, figs. 5 & 6, which together with fig. 7 show three sections of a chick of 7th day[1], that there is a horizontal ridge of the same nature on the left side also (γ, γ), where of course there is no vena cava inferior.

Later stages in the development of this septum are shown in the series of transverse sections of embryo of 10th day (figs. 20, 21, 22, γ, γ), and in the transverse sections of 12th day (figs. 27 & 28, γ, γ).

It will be seen that the growth of the abdominal air-sacs has considerable influence on the development of this septum, into which they extend from its outer anterior border. We may say in fact that though a starting-point is supplied by the ridge (γ) which is visible as a backward continuation of the pulmonary mesoblast in the earliest stages, it is only when the abdominal air-sacs have attained some degree of development (as at about the time of the completion of the avian diaphragm, 9th to 10th days), that a true septum reaching from the lateral walls to the median vertical mesentery (*cf.* fig. 22, γ, γ) is apparent and begins to extend posteriorly and obliquely ventralwards.

This oblique abdominal septum, or anterior and dorsal portion of the *post-hepatic septum*, is shown in its adult relations in figures 45 and 46, γ, γ (transverse sections).

The ventral part of the latter is formed by the laterally extended ventral ligament of the gizzard and hinder part of liver, which goes by the names of gastrohepatic ligament and the great omentum.

We see this membrane in the longitudinal-vertical section of 10th day (taken to the right of the middle line, wherefore the gizzard does not appear) (fig. 18, β) extending from the ventral body-wall to the posterior side of the liver. It is shown also in figs. 13, 17, 19, 20, 26, 27, 28, and also in 29, β, β. Further, I would call attention to fig. 16, which is a longitudinal-horizontal section through the more dorsal part of the gall-bladder (*b.g*) and the antero-ventral corner of the lung (*pul.*) of a chick of the 12th day. On the right

[1] Owing to the curvature of the embryo at that date, these are partly horizontal-longitudinal and partly transverse. They are very similar to figures 581 and 582 in Duval's Atlas; but the latter fail to show the presence of the ridge γ on the left side.

side there is still a communication (*) between the hepatic and post-hepatic parts of the abdominal cavity; and comparing this with figs. 15 & 17, which represent sections respectively dorsal and ventral to the section in fig. 16, it will be seen that the more dorsal part of the *post-hepatic septum* is composed of the *oblique abdominal septum* (γ), while the more ventral part consists of the lateral "omental" extension (β). On the left side the ventral and dorsal components of the *post-hepatic septum* never meet, and there is always in the fowl a free communication between the "pulmohepatic recess" of this side and the general intestinal cavity. In the duck this is reduced to the condition of a small aperture (*cf. suprà*, p. 454).

With regard to the origin of this post-hepatic septum, it would seem that the ventral portion (β) is, so to speak, started by the vitelline veins which cause considerable inward projections of the lateral body-walls in which they run. With the closing-in of the body-wall in the region of the umbilicus, the vessel of the left side which alone continues as the allantoic vein (or in the adult as an anterior abdominal vein carrying blood from the fat-laden omentum) comes to assume a more central course, but the ventro-lateral attachment of the membrane which supported these vessels persists.

The dorsal component (γ) of the *post-hepatic septum*, on the other hand, is due to the extension laterally and posteriorly, by the growth of the abdominal air-sacs, of the ridge that forms a backward continuation of the pulmonary tissue of either side. And it is thus that I believe that in those Sauropsida which have no similar arrangement of air-sacs the post-hepatic septum, which may be present (Crocodiles and Teiidæ), is the homologue of the ventral component of this septum in the bird—the dorsal part being merely represented by the membranous fold, which in many Lizards extends for a considerable distance behind the lungs.

IV. On the Body-cavity of the Lacertilia and of the Teiidæ in particular.

(*a*) *The Lacertilia generally.*

Turning now to the Lacertilia and recurring to the question of the ventral attachment of the lungs. The *left* lung seems to have, as a rule, its ventral border but slightly if at all attached, but there is sometimes a short ligament connecting this with the liver or tissue in front of that organ.

The right lung, on the other hand, seems as a rule (*cf.* p. 465, fig. A) to have its whole ventral border attached to the dorsal wall of the right liver-lobe, or—seeing that dorsally it is attached to the middle line by another ligament—it may sometimes be rather described as set on the outer side of a membrane passing between the right liver-lobe and the dorsal part of the median mesentery. The spaces thus enclosed between the lung and its ligaments on the outside, and the œsophagus and its ligaments in the middle line, are homologous with the *pulmohepatic recesses* of birds above described

(*cf.* Plates XLVI.–XLIX. figs. 1–4 and woodcut A, p. 465), and the membranes between the lung and liver are the *pulmohepatic ligaments*.

The ligaments of the right side and consequently the corresponding *recess* is fully developed in the following genera :—

Lacerta (*viridis, muralis*).	*Uromastyx*.
Iguana (*tuberculata*).	*Chamæleon*.
Gerrhosaurus (*flavigularis*).	*Sphenodon*.
Goniocephalus (*sophiæ*).	*Trachidosaurus*.

In the last-named genus the posterior end of the lung is attached by a separate membrane to the ligament between the liver and dorsal wall.

The Teiidæ are the only family in which I have met with the condition in which the lung of each side is suspended freely by its more dorsal ligament, with a consequent absence of *pulmohepatic recess*.

This condition is visible in the following, which are the only representatives of the family that I have examined :—

Tupinambis (*teguixin*) (*Tejus teguexim*, Gray).
,, (*nigropunctatus*).
Ameiva (*surinamensis*).
Callopistes (*maculatus*).

The two types of lung-suspension referred to may be thus diagrammatically represented [1] :—

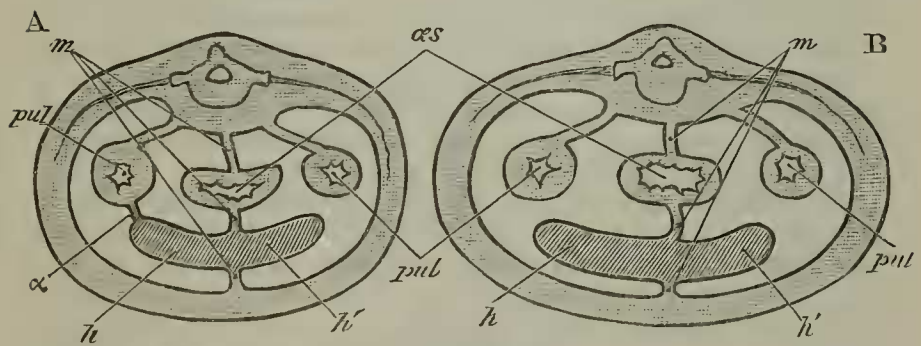

Fig. A. Diagrammatic section of one of the lizards included in the first list given above, taken through the lungs and liver.
Fig. B. A similar section of one of the Teiidæ, mentioned in the second list.
a, pulmohepatic ligament; *œs*, œsophagus; *h*, *h'*, right and left liver-lobes; *m*, median thoracic septum; *pul*, lung.

A second set of attachments of the liver frequently met with are ventral ligaments that run outwards from the pericardium, or the

[1] It may be noted that two similar types occur among the Amphibia. Thus, in the Salamander all the membranous attachments of the lungs and liver seem to be precisely similar to those in the common Lacertilian type (*e.g. Lacerta*). But in the Frog the two lungs hang freely suspended on either side, as in the Teiidæ.

median ventral ligament behind it, and take a more or less oblique course across the liver. Sometimes there is more than one such on a side.

I would call these the *oblique ligaments* of the liver.

These ligaments, when present, appear, in certain cases, to be continuous with the membranes that bear the forward continuations of the Müllerian ducts (oviducts), and are specially noticeable in the case of the Chameleon, where they form broad sheets of membrane constituting a kind of ventral diaphragm [1].

The oblique ligaments can be traced in *Lacerta*, *Uromastyx*, *Ameiva*, *Chamæleon*, and others, but their number, distribution, and degree of development is different in different forms; and I call attention to them chiefly on account of the light they may throw on the nature of certain membranes in the Crocodiles. There are in these animals (*cf.* p. 469) certain well-defined ventral ligaments of the liver, which completely mark off the more median portion of each lobe from its antero-lateral corner, and seem to correspond to these inconspicuous ligaments in the Lacertilia, but not truly to anything in Birds.

I am inclined to regard such oblique ligaments as complementary to the pulmo-hepatic ligaments; that is, to consider that they serve to unite the liver to the body-wall in those forms in which the tissue corresponding to the avian diaphragm, to which the last-mentioned ligaments are attached, does not itself become attached to the body-wall.

The more or less marked folds of peritoneum, which carry the forward continuations of the Müllerian ducts, seem (*cf.* p. 462) to mark the line along which an avian diaphragm might be expected to arise; and they probably exercise one of the functions of a diaphragm, in rendering a certain protection to the lungs; but I would not advocate any closer homology between these membranes and the diaphragms of either Birds or Mammals.

The relation of the lungs to the body-cavity in the Monitors is referred to in my paper on the "Fat-bodies," to be subsequently read, and I have nothing further to add here.

(*b*) *The Teiidæ.*

The condition in *Tupinambis teguixin* (*Tejus teguexim*, Gray) is very interesting.

We have here (*cf.* Plate XLVIII. figs. 31–34) a post-hepatic septum (β), apparently homologous with the ventral (or so-called "omental") portion of the post-hepatic septum in birds (the ventral side of which is shown in fig. 29, β), and perhaps to the greater part of the post-hepatic septum in Crocodiles (figs. 40–43, β).

This well-marked post-hepatic septum at first strikes the observer

[1] Such oblique ligaments do in their adult relations rather suggest part of the embryonic mammalian diaphragm. They attach the liver to the body-wall posteriorly and ventrally to the attachment of the liver to the lungs or mediastinum (compare with this Plate XLVI. fig. 4, *dph.*).